University of Nebraska - Lincoln
DigitalCommons@University of Nebraska - Lincoln

Faculty Publications in the Biological Sciences | Papers in the Biological Sciences

2001

Rhinocyllus conicus: Initial Evaluation and Subsequent Ecological Impacts in North America

A. Gassmann
CABI Bioscience Centre Switzerland

Svata M. Louda
University of Nebraska - Lincoln, slouda1@unl.edu

Follow this and additional works at: https://digitalcommons.unl.edu/bioscifacpub

 Part of the Life Sciences Commons

Gassmann, A. and Louda, Svata M., "*Rhinocyllus conicus*: Initial Evaluation and Subsequent Ecological Impacts in North America" (2001). *Faculty Publications in the Biological Sciences*. 100.
https://digitalcommons.unl.edu/bioscifacpub/100

This Article is brought to you for free and open access by the Papers in the Biological Sciences at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Faculty Publications in the Biological Sciences by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

8

Rhinocyllus conicus: Initial Evaluation and Subsequent Ecological Impacts in North America

A. Gassmann[1] and S.M. Louda[2]

[1]CABI Bioscience Centre Switzerland, CH-2800 Delémont, Switzerland; [2]School of Biological Sciences, University of Nebraska, Lincoln, NE 68588-0118, USA

Abstract

Renewed debate over the risk of non-target effects in biological control reflects, in part, the recent quantification of direct and indirect ecological effects of the flowerhead weevil, *Rhinocyllus conicus* Fröl., in North America. To help resolve the issue, we review the published data for *R. conicus* from both Europe and North America: pre-release (1961–1968), post-release (1969–1985) and more recent (1986–1999). Our aim was to determine the extent to which host range expansion on to native North American species, and the associated ecological effects, were predicted or predictable. Our overall conclusion is that more was known than is generally realized, yet more information would have been required to complete the initial assessment of ecological consequences. Three important points emerge. First, the potential effect of *R. conicus* on native North American species was not a major element of the testing programme. Second, the host range expansion observed is consistent with the pre-release and early post-release data, and so was predictable, if not predicted. The pre- and early post-release data showed that *R. conicus* could feed and develop on multiple *Cirsium* species, including two North American species. Third, we found that the studies needed to quantify the likely magnitude of feeding by *R. conicus* on North American *Cirsium* species, and thus the ecological consequences of that feeding, were not done. Instead, inferential arguments were used to suggest that any feeding by *R. conicus* on North American species would not be substantial. We conclude that there were sufficient data, which suggested that North American *Cirsium* species would be acceptable

© CAB *International* 2001. *Evaluating Indirect Ecological Effects of Biological Control* (eds E. Wajnberg, J.K. Scott and P.C. Quimby)

host species, to have warranted further testing to define and quantify the potential ecological side-effects of introducing *R. conicus* to North America. Contemporary concerns should now mandate such tests.

Introduction

The risks associated with the practice of biological control, especially the potential for harmful ecological effects on non-targeted native species, are being debated again (see Secord and Kareiva, 1996; Simberloff and Stiling, 1996, 1998; Frank, 1998; Thomas and Willis, 1998). The issue is not new (e.g. Simberloff, 1981, 1992; Howarth, 1983, 1991). In fact, the importance and the need of doing more quantitative evaluations of potential risk to non-target native species was argued by several biological control practitioners over 15 years ago (Andres, 1985; Pemberton, 1985a,b; Turner, 1985). Several countries, such as Australia and New Zealand, have instituted a clear legislative process to identify risks, to involve all affected parties and to ensure that non-target impacts are minimized (New Zealand Government, 1994; Withers *et al.*, 2000).

In this chapter, we will review the evidence available to evaluate the specific case of the introduction of *Rhinocyllus conicus* Fröl. (Fig. 8.1) into North America. This Eurasian weevil was released for the biological control of true thistles, especially those in the genus *Carduus*. Recent evidence that

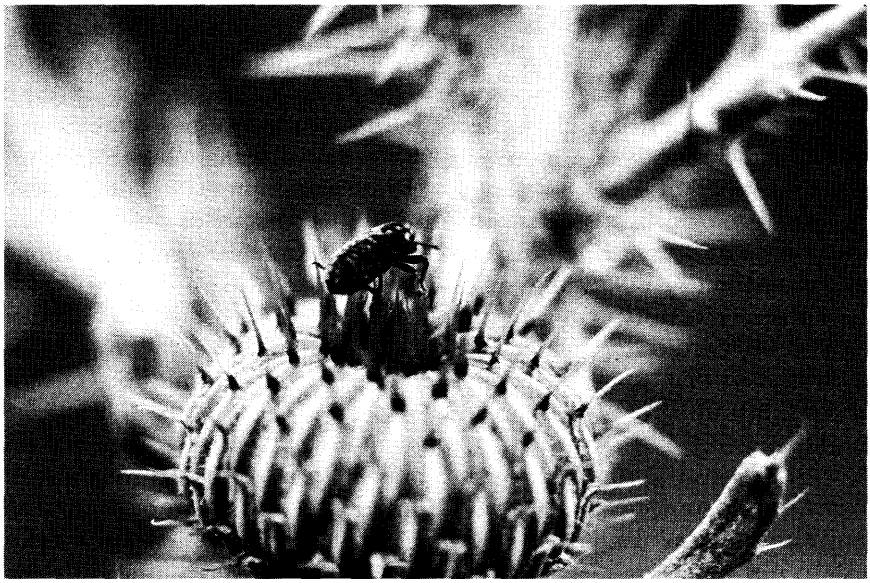

Fig. 8.1. *Rhinocyllus conicus* on Platte thistle (*Cirsium canescens* Nutt.) at Arapaho Prairie, Arthur County, Nebraska, USA.

R. conicus populations are increasing in nature preserves and National Parks in the central USA (Louda *et al.*, 1997, 1998; Louda, 1998), and that these populations are having a significant impact on native plant and insect species within the preserves (Louda *et al.*, 1997; Louda, 2000a; Louda and Arnett, 2000), has rekindled earlier apprehensions about the environmental safety of classical biological control (Howarth, 1991; Secord and Kareiva, 1996; Simberloff and Stiling, 1996).

Specifically, we will examine the evidence developed on this insect and its host plant interactions in Europe before, and in the 15 years after, its release in North America. Then, we will summarize the more recent findings. Thus, our purpose is to determine the extent to which the host range expansion on to native North American *Cirsium* species, and the ecological effects recently associated with this expansion, were predicted or predictable from the published data used to evaluate economic and environmental risk. Our overall conclusion for this case is that more was known than is generally realized, and yet more information would have been required to effectively assess potential ecological consequences.

The common name 'thistle' is customarily applied to species in the Tribe *Cardueae* of the *Asteraceae* (*Compositae*), and the term 'true thistle' is sometimes used to refer to the spiny species of the Subtribe *Carduinae*. Some ten different 'true thistle' species in four genera of western Palaearctic origin (*Carduus, Cirsium, Silybum* and *Onopordum*) have been accidentally introduced into North America, Australia and New Zealand (Julien and Griffiths, 1998). No native *Carduus* species occur in North America and most indigenous Nearctic true thistles belong to the genus *Cirsium*. The *Carduus nutans* group is taxonomically difficult, and it includes several species or subspecies (Desrochers *et al.*, 1988). In this chapter, we use *C. nutans* L. to refer to all of the taxa in this complex group.

In North America, the weediness of exotic true thistles was viewed as an agronomic problem (e.g. Dunn, 1976; McCarty, 1978). So, both the US Department of Agriculture (in 1959) and the Canadian Department of Agriculture (in 1961) initiated biological control programmes against exotic thistles, starting with broad surveys of the insects and pathogens on the *Cardueae* in Europe (Zwölfer, 1965; Boldt, 1978; Dunn, 1978). Between 1961 and 1966, 2283 populations or stands of 16 genera in the tribe, including 1354 in the Subtribe *Carduinae*, were surveyed from western France to eastern Austria, and from southern Germany to northern Italy and northern former Yugoslavia (Zwölfer, 1965). Over 120 species of insects were associated with true thistles in the genera *Carduus, Cirsium, Silybum* and *Onopordum* in the western portion of their indigenous Eurasian range (Zwölfer, 1965; Redfern, 1983). Boldt (1978) reported that some 40 insects were endophytic on *C. nutans* in Italy. On the basis of the surveys and early tests, *R. conicus* was selected as the first agent to be released in North America for the biological control of exotic thistles, especially those in the genus *Carduus*. Weevils, collected in the upper Rhine Valley

in eastern France, were first released in Canada in July 1968 on musk (nodding) thistle (*C. nutans*) near Regina, Saskatchewan, and on plumeless thistle (*Carduus acanthoides* L.) near Belleville, Ontario (Harris and Zwölfer, 1971). In 1969, introductions from eastern France began in the United States, with releases in California, Montana, Nebraska and Virginia (Hawkes *et al.*, 1972; Kok, 1974; Kok and Surles, 1975; Rees, 1977, 1978, 1982, 1991; McCarty, 1978; Surles and Kok, 1978; McCarty and Lamp, 1982). In Nebraska, weevils from Mulhouse, France, and possibly some from Rome, Italy, were released in 1969 and between 1972 and 1974 on *C. nutans* near Lincoln and Grand Island (McCarty, 1978; L.A. Andres, unpublished results). The weevil was then actively redistributed in southern and eastern Nebraska (McCarty and Lamp, 1982). Redistribution of *R. conicus* in the United States continues (e.g. Boldt and Jackman, 1993; Buntin *et al.*, 1993).

The history of research on *R. conicus* in Europe and North America can be divided into three periods, including the pre-release period of research in Europe (1961–1968), the early post-release period (1969–1985) and the more recent period of research (1986–1999). After reviewing the natural history of *R. conicus*, we will summarize the findings relevant to evaluation and prediction of post-introduction performance from each of these periods. We will then address the general question of whether the state of knowledge at pre-release and early post-release was sufficient to predict both the occurrence of feeding and the magnitude of ecological impact by *R. conicus* on native thistles and their adapted floral insects. We contend that such retrospective studies can be used to evaluate and improve future efforts in biological control.

Natural history of *Rhinocyllus*

The indigenous geographical distribution of *R. conicus* includes central and southern Europe and North Africa (Hoffmann, 1954), as well as Asia Minor (Schaufuss, 1915). Preferred habitats of thistles in Europe, according to Zwölfer (1964), are in dry and warm localities below elevations of 600 m. Mating and oviposition activity occur in spring and early summer, following adult emergence from overwintering in litter and sheltered sites and a pre-oviposition feeding period of varying length. Eggs are laid externally, either individually or in small clusters, on the lower surface of the involucral bracts of young flowerheads (Rees, 1977, 1982; Zwölfer and Harris, 1984). The life cycle is well documented. Larvae feed on the florets, the developing receptacle, callus tissue produced near the feeding site (Shorthouse and Lalonde, 1984), and sometimes into the peduncle under the head (Zwölfer and Harris, 1984). At the end of the fourth instar, the larva forms an ovoid cell with hard, frass-packed, black walls and pupates (Shorthouse and Lalonde, 1984; Zwölfer and Harris, 1984). Development,

from egg to teneral adult, took 45–55 days in the Swiss Jura (Zwölfer and Harris, 1984) and 39–62 days in the Gallatin Valley, Montana, USA (Rees, 1982). Teneral adults usually remain within the pupation cells for several weeks before dispersing to find overwintering sites (Zwölfer and Harris, 1984). The number of generations per year can vary, from one in the Apennine Mountains of Italy (Mellini, 1951) and southern Europe (Aeschlimann, 1999), to a partial second generation in the upper Rhine Valley and eastern Austria in central Europe (Zwölfer, 1967).

In Europe, *R. conicus* overlaps with a large number of floral herbivores (Zwölfer, 1965) that may cause substantial mortality (Zwölfer, 1978, 1979). For example, in flowerheads with either *Urophora solstitialis* L. (Tephritidae) or *Larinus sturnus* Schall. (Curculionidae), *R. conicus* mortality averaged 70–90% (Zwölfer, 1978; Zwölfer and Harris, 1984). In North America, larval survivorship is strongly density-dependent (Surles *et al.*, 1975; Rees, 1977; Dowd and Kok, 1981a; Goeden and Ricker, 1985), suggesting that intraspecific competition can cause larval mortality (> 80%) within heavily infested inflorescences.

The natural enemy complex is extensive in both Europe and North America. In Europe, Zwölfer and Harris (1984) listed six larval and pupal parasites, plus an egg parasitoid (Mellini, 1951). Parasitism levels in Europe were high, especially by *Bracon* sp. (43–71%), *Bracon urinator* L. (40–50%) and *Exeristes roborator* F. (13–43%). Natural enemies reported in North America include: parasitoids (1 adult, 10 larval-pupal), predators (a reduviid, a neuropteran, salticid and thomisid spiders) and parasites (a mite, two bacteria and a fungus) (Goeden and Ricker, 1977, 1978; Dowd and Kok, 1981b). Reported levels of parasitism in the USA are very low (< 3%) (Surles, 1974; Surles *et al.*, 1975; Goeden and Ricker, 1977; Rees, 1977; Puttler *et al.*, 1978; Dowd and Kok, 1981a, 1982, 1983; Smith and Kok, 1983). Finally, some intra-guild predation occurs in Europe. Two lepidopterans that develop on floral tissues and achenes within *C. nutans* flowerheads (Pyralidae: *Homoeosoma nebulellum* Hb., *H. binaevellum* Hb.) reportedly also feed on any insect larvae that they encounter, including those of *R. conicus* (Zwölfer, 1978). In North America, related lepidopteran larvae (*Homoeosoma* spp.) occur within flowerheads of native *Cirsium* species (Lamp and McCarty, 1981; Louda and Potvin, 1995; G. Balogh, personal communication). Rees (1977, 1978) found no evidence of feeding by *Homoeosoma electellum* (Hulst.) on *R. conicus* in Montana, but no direct test has been done.

Pre-release studies in Europe (1961–1968)

Study of *R. conicus* as a potential biological control agent for exotic thistles in North America, particularly *Carduus* species, included both field studies of occurrence and host use and laboratory studies of adult behaviour and

larval performance. Zwölfer and Harris (1984) synthesized most of the results for *R. conicus* available before 1984.

Early field studies

Field collection records of *R. conicus* in Europe (Table 8.1) show that eggs or larvae of *R. conicus* were found on five out of nine *Carduus* species (55.6%) and two out of 16 *Cirsium* species (12.5%), as well as on *Silybum marianum* (L.) Gaertner and *Onopordum acanthium* L. (Zwölfer, 1967). Adults were also found on *Carduus sanctae-balmae* Lois, at Toulon in southern France, and on *Cirsium vulgare* Ten., at Nantes in western France and at Châteauroux in central France, but not on *C. vulgare* in eastern France or in the Rhine Valley. *R. conicus* larvae and adults were found on *C. nutans* everywhere except in southern France and north-eastern Spain. Other host plants in the literature included *Galactites tomentosa* Moench and four more *Cirsium* species: *Cirsium eriophorum* (L.) Scop., *Cirsium canum* (L.) All., *Cirsium anglicum* Lob. and *Cirsium chrysacanthum* Ball. These literature records, however, could not be confirmed in the early surveys (Zwölfer, 1965; Zwölfer and Harris, 1984).

The field records for Europe suggested a clear preference of *R. conicus* for *Carduus* species over other accepted plant species. Zwölfer (1967) pointed this out:

> The genus *Carduus* is by far preferred over the host genera *Cirsium*, *Silybum*, or *Onopordum*. The genus *Cirsium* has been investigated much more intensively than the genus *Carduus*, but nevertheless 75% of the records of adults and 80% of the records of larvae of *R. conicus* originate from *Carduus* species.

R. conicus was observed on three out of 16 *Cirsium* species investigated. The percentage of samples containing eggs or larvae of *R. conicus* varied from 20 to 60% within the genus *Carduus*, below 5% in the genus *Cirsium*, and below 10% in the genera *Silybum* and *Onopordum*. Unlike for *Larinus* spp., no evidence of intraspecific differentiation was observed. So, Zwölfer (1967) suggested that regional differences in host plant association of *R. conicus* could be related to host preference and phenology.

Population phenology of *R. conicus*, initiated by adult emergence from overwintering sites, varies with latitude and elevation within Europe and the Mediterranean. For example, in the upper Rhine Valley in the north, Zwölfer (1964, 1967) found that *R. conicus* adults were active from the first half of May, when they were abundant, until August. Larvae were found in flowerheads from late May until August, and pupae occurred from mid-July to September (Zwölfer, 1964, 1967; Zwölfer and Harris, 1984). A partial second generation sometimes occurred for individuals that completed development early, when day length was greater than 16 h (Zwölfer, 1967; Zwölfer and Harris, 1984). Additionally, in the Apennine Mountains north

of Florence, Mellini (1951) observed a relatively late onset of all stages: oviposition in early July, larval development in July/August and pupation in late August. In the Mediterranean climate region, for example near Toulon and Orange in southern France and Gerona in northern Spain, Zwölfer (1967) found over-wintered *R. conicus* adults emerging very early, from mid-April, and eggs were found from early May. In summary, *R. conicus* in the Mediterranean climatic area were active several weeks ahead of those in the more continental areas or higher elevations, and they were reported to have a shorter activity period.

Early laboratory studies of host acceptance, preference and performance

The plant species tested in the screening trials included primarily cultivated plants, agricultural crops and horticultural species, plus European thistles (Zwölfer, 1964, 1967, 1969; Zwölfer and Harris, 1984). All the tests were made with field-collected adults originating from *C. nutans* from eastern France. In no-choice feeding tests, where adult weevils were offered leaves of a potential host plant, no feeding occurred on the cultivated non-*Astereae*, but 12 of the 16 European species of *Carduinae* offered were fed upon. One North American *Cirsium* (*Cirsium undulatum* Spreng.) was screened in one small adult feeding trial in Canada (n = five weevils). The leaves of this species were accepted, but only at the 'slight and inconsistent feeding' level (Zwölfer, 1967), the same level as European *Carduus tenuiflorus* Curtis, *S. marianum* and *O. acanthium* (Zwölfer and Harris, 1984). Interestingly, the five weevils in this trial on *C. undulatum* died more rapidly than did those on the leaves of other thistles tested (Zwölfer, 1967; Zwölfer and Harris, 1984).

Some feeding was noted in preference (i.e. 'choice') tests, where adult weevils were offered leaves of both *C. nutans* and another plant in the Tribe *Cardueae*, i.e. *Carlina vulgaris* L., *Carthamus tinctorius* L. and *Cnicus benedictus* L., as well as 12 of 14 species in the Subtribe *Carduinae* (Zwölfer, 1964). Among the *Carduinae*, two results are striking. First, the preference for two (16.7%) of the 12 species (*Carduus crispus* L., *Cirsium acaule* (L.) Scop.) was actually greater than that for *C. nutans*. Second, the thistles fell into two groups. The highly preferred group included (in rank order): *C. crispus*, *C. acaule*, *C. nutans* and *Cirsium vulgare*. The less preferred group included (in rank order): *Cirsium arvense* (L.) Scop., *Cirsium rivulare* (Jacq.) All., *Cirsium palustre* (L.) Scop., *Carduus personata* (L.) Jacq., *S. marianum*, *Cirsium oleraceum* (L.) Scop., *Carduus tenuiflorus* and *O. acanthium* (Zwölfer, 1964). These two groups are clearly not defined by host plant genus.

In oviposition and larval development tests, the data included records of eggs laid in laboratory feeding trials on leaves, and a no-choice field test of oviposition and development. The latter test was done in the garden at Delémont, Switzerland, on four of the eight European thistles with

Table 8.1. Field records of *Rhinocyllus conicus* (modified from Zwölfer, 1965, 1967; Zwölfer and Harris, 1984).

	1961–1966			1961–1982		
	Populations sampled	% samples with larvae[a]	% samples with adults[a]	Populations sampled	% samples with larvae[a]	% samples with adults[a]
Echinopinae						
Echinops (4 spp.)	25	0	0	41	0	0
Carlinae						
Carlina (3 spp.)	85	0	0	158	0	0
Xeranthemum (1 sp.)	5	0	0	7	0	0
Centaureinae						
Serratula (1 sp.)	16	0	0	17	0	0
Centaurea (17 spp.)	750	0	0	950	0	0
Microlonchus (1 sp.)	8	0	0	11	0	0
Crupina (2 spp.)	5	0	0	6	0	0
Leuzea (1 sp.)	5	0	0	9	0	0
Carthamus (1 sp.)	30	0	0	47	0	0

Carduinae						
Arctium (4 spp.)	60	0	0	106	0	0
Jurinea (1 sp.)	—	—	—	2	0	0
Staehelina (1 sp.)	5	0	0	8	0	0
Galactites (1 sp.)	10	0	0	12	0	0
Carduus nutans	109	57.5	60.0	157	49.0	50.3
C. nigrescens	3	33.3	100.0	3	33.3	100.0
C. personata	25	33.0	38.0	28	35.7	42.9
C. crispus	20	40.0	20.0	30	26.7	13.3
C. sanctae-balmae	6	0	50.0	6	0	50.0
C. pycnocephalus	12	20.0	30.0	17	23.5	35.3
C. acanthoides	39	0	0	55	0	3.6
Two other *Carduus*	40	0	0	44	0	0
Cirsium vulgare	142	0	0.8	225	6.2	7.1
C. palustre	47	4.0	0	60	3.3	0
C. setosum	—	—	—	3	33.3	0
C. arvense	475	3.5	4.0	550	2.9	3.8
13 other *Cirsium*	300	0	0	356	0	0
Silybum marianum	14	8.0	0	23	17.4	26.1
Cynara scolymus	—	—	—	4	0	0
Onopordum acanthium	42	5.0	10.0	47	4.2	8.5
Two other *Onopordum*	5	0	0	19	0	0

[a]Percentage of local populations sampled for the presence of larvae or adults of *R. conicus*.

R. conicus oviposition recorded from the field: *Carduus nutans*, *C. personata*, *Cirsium arvense* and *C. palustre*. Each of these species supported complete development. Zwölfer (1967) noted that 'The adults emerging from *C. arvense* and *C. palustre* were, however, about 10% smaller than their parents which originated from *C. nutans*'. Thus, this early screening trial showed that the two European *Cirsium* species were adequate hosts, even though they were much less preferred than *C. nutans* in adult feeding trials (Zwölfer, 1964). No oviposition tests or larval development tests were carried out on any North American *Cirsium* species. Also, no multiple-choice oviposition preference and larval development tests were done to determine the relative ranking of potentially acceptable European or North American thistle species.

In summary, the early trials substantiated that feeding by *R. conicus* was restricted to the Subtribe *Carduinae*, and they suggested that some species of acceptable thistle host plants were preferred over others. Since none of the agricultural crops and horticultural species tested was used by the weevil, the decision was taken by the Canada Department of Agriculture and the US Department of Agriculture, Agricultural Research Service, to release the weevil on exotic thistles in Canada (*C. nutans*, *C. acanthoides*) and in the United States (*C. nutans*, *S. marianum*). Redistribution of *R. conicus* continued, even though some feeding on non-target *Cirsium* species was recorded very early and there was 'considerable opposition to the introduction to North America of biocontrol agents for thistles on the grounds that they may also damage native *Cirsium* spp.' (Zwölfer and Harris, 1984).

Early post-release studies (1969–1985)

After release, studies of the host associations of *R. conicus* in Europe were continued, and studies of the biology and feeding of *R. conicus* on its targeted host plants were done in North America.

Field studies in Europe

Additional surveys were carried out during 1981 (see Table 8.1). The patterns were consistent with the previous studies, although *R. conicus* adults were also documented on *Carduus acanthoides*. In addition, the rate of attack recorded on *Cirsium vulgare* was higher than previously, most likely because sampling increased in south-western France. Occurrence of *R. conicus* on *C. vulgare* was higher in south-western France than in north-eastern France, Austria and Germany (Zwölfer and Preiss, 1983). In total, 4 out of 17 *Cirsium* species (23.5%), and seven out of nine *Carduus* species (77.8%), were recorded as hosts of *R. conicus* during 1981. The phenology of *R. conicus* in North America was quantified and also found to vary with

latitude, with earlier emergence and activity in the south. In the Gallatin Valley of Montana, USA, overwintered adults were observed aggregating and mating on musk thistle (*C. nutans*) from mid to late May, and newly emerged adults were found primarily in late July and early August (Rees, 1982). Alternatively, further north, newly emerged adults were observed in late July to early August in southern Ontario, but not until August in Saskatchewan (Harris, 1984).

A major change occurred during this period in the general interpretation of the variation in host plant association of *R. conicus* in the field. Before *R. conicus* was released in Canada in 1968, host preference and possibly host phenology were thought to determine host association (Zwölfer, 1967). However, by 1984, ecotypic differentiation among host-related strains ('biotypes') of *R. conicus* was widely, if not universally, accepted as the main determinant of host association (Zwölfer and Harris, 1984). This shift was initiated by Goeden's (1978) observation that the response of *R. conicus* to its host plants in southern California varied. Weevils from *Carduus pycnocephalus* L. consistently preferred to oviposit on *C. pycnocephalus*, whereas those from *S. marianum* preferred *S. marianum*. Goeden (1978) hypothesized that two 'host races' of *R. conicus* existed in California. He then hypothesized that the earlier attempt to establish *R. conicus* on milk thistle (*S. marianum*) in northern California (Hawkes *et al.*, 1972) had failed because the weevil biotype and weed species were mismatched (Goeden, 1978; Goeden *et al.*, 1985).

In Europe, Goeden's hypothesis stimulated a re-assessment of host records for *R. conicus*. Zwölfer and Preiss (1983), for example, also concluded that *R. conicus* was divided into five 'host race' biotypes: (i) *S. marianum* biotype; (ii) *Carduus nutans* biotype, also occasionally found on *Cirsium* spp., which was the most widespread and presumably most ancient biotype, (3) *Carduus pycnocephalus* – *C. tenuiflorus* biotype; (iv) *Cirsium arvense* biotype, which was rare in Europe; and (v) *Cirsium vulgare* biotype in western France, which was also occasionally found on *Carduus nutans*. Thus, Zwölfer and Preiss (1983) rejected the weevil – host plant synchrony hypothesis (Zwölfer, 1967) to explain variation in host plant use among regions, and they accepted the innate preference hypothesis instead. They suggested that preference was driven by selection for resource predictability, consistent with the resource concentration hypothesis (Root, 1973), and this determined host plant association and its geographical variation.

At this point, definitive evidence for five clearly differentiated, genetic host races (biotypes) was not available, and some conflicting evidence existed. For example, *R. conicus* from *Cirsium vulgare*, evaluated in a multiple-choice oviposition test, unexpectedly laid as many eggs on *Carduus nutans* as they did on *Cirsium vulgare* (Zwölfer and Preiss, 1983). Also, Jessep (1981) reported that, in New Zealand, *R. conicus* from Canadian *Carduus nutans* successfully colonized *Carduus pycnocephalus*, *C. acanthoides* and *C. tenuiflorus*, as well as *C. nutans*. Moreover, the role of interspecific variation

in the availability of flowerheads was not evaluated, even though it was known that intraspecific variation in flowerhead size influenced oviposition in both *S. marianum* and *C. vulgare* (Zwölfer and Preiss, 1983).

It seems clear that the wide acceptance of host-plant biotypes, and perhaps of resource concentration, as predictive of host use, had a major influence on the interpretation of the data. These perspectives lead to the expectation of insignificant levels of non-target feeding on native North American *Cirsium* species by *R. conicus* from *C. nutans*. The existence of host-plant biotypes in *R. conicus* has been challenged recently (Klein, 1991; Klein and Seitz, 1994).

Laboratory and greenhouse studies of preference and performance in North America

Kok and his colleagues in Virginia experimentally substantiated the oviposition preference of *R. conicus* from *C. nutans* in Europe for *C. nutans* over *C. acanthoides* in its new environment (Surles and Kok, 1977), as expected. They found that oviposition was better synchronized with *C. nutans* than with *C. acanthoides* in Virginia. Also, larval crowding decreased survival more in the smaller flowerheads of *C. acanthoides* than in the larger ones of *C. nutans* (Dowd and Kok, 1981a). Second, Smith and Kok (1985) found that temperature influenced larval development and mortality. The threshold temperature for hatching was 11°C, and the threshold temperatures for development were between 16 and 20°C, depending on the stage. Third, Dowd and Kok (1983) documented the influence of plant quality on weevil success. In the greenhouse, weevils developing in flowerheads of musk thistle (*C. nutans*) plants that were fertilized or well-watered, compared with unfertilized or dry, tended to survive better and they developed into significantly larger adults. Also, phytosterols (especially sitosterol), which are found in highest concentrations in the flowerhead buds, were necessary for complete larval development on artificial diets (Rowe *et al.*, 1985). These studies suggested that preference and synchronization, based on physical conditions and host plant quality, could influence host plant use by *R. conicus* in the field in North America.

Garden plot and field studies in North America

In Canada, field studies showed that oviposition was concentrated at the beginning of the flowering season. Although egg distribution was aggregated, the larval distribution was even more aggregated, and the degree of aggregation varied significantly among years (Zwölfer and Harris, 1984). Variance-to-mean ratios ranged from 1.84 to 7.99 in pasture and from 1.0 to 11.37 in gravel spoil plots over the first 10 years. Also, the maximum

number of *R. conicus* maturing in a *C. nutans* head was correlated with its size. Growing conditions again appeared important. For example, the degree of aggregation was inversely correlated with spring soil moisture. Day length affected the development of a second partial generation. Newly developed adults that had emerged early, by mid-June (> 16 h light), were observed mating. Finally, a low incidence of parasitism by a wide variety of larval and pupal parasitoids was reported in Canada (Zwölfer and Harris, 1984).

In Virginia, establishment by the *R. conicus* imported from *C. nutans* in eastern France was more successful on *C. nutans* than on *C. acanthoides* (Kok, 1974; Surles *et al.*, 1974; Kok and Surles, 1975), possibly due to synchrony. Total mortality for all immature stages of *R. conicus* on *C. nutans*, at 11 release sites in Virginia, averaged 68%, ranging from 56.6% to 95.3% (Surles *et al.*, 1975). Egg and early instar larval mortality (58.3%) was caused primarily by wind and rain. Late larval and pupal mortality (9.7%) was caused by parasitism (3.6%), larval crowding and unknown factors (Surles *et al.*, 1975). In both 1973 and 1974, weevils reduced the number of viable seeds in the terminal and first lateral heads and total seed production by 35–36% per *C. nutans* plant. However, they only reduced viable seed by 0.2% per *C. acanthoides* plant, due to low infestation rates (Surles *et al.*, 1974; Surles and Kok, 1978). A phenological model of the interaction of *R. conicus* with *C. nutans* in Virginia (Smith *et al.*, 1984) demonstrated that temperature could have a major influence on the synchrony of the host plant and weevil, and so on the magnitude of their interaction.

In California, Goeden (1978) and Goeden and Ricker (1977, 1978) found evidence consistent with the host race hypothesis. *R. conicus*, collected from *S. marianum* in southern Italy, established successfully on *S. marianum* in southern California (1971–1974), even though earlier releases of weevils from *C. nutans* in eastern France had failed to establish on *S. marianum* in northern California (Hawkes *et al.*, 1972; Goeden, 1978). In 1978, another establishment of the southern Italian form of *R. conicus* was made on *S. marianum* in Fall County, Texas, USA, using weevils from *S. marianum* in California (Boldt and DeLoach, 1985). Clearly, these observations suggest that genetic variation occurs among populations of *R. conicus*. Interpretation of how that variation is partitioned is now being revised (Klein, 1991; Klein and Seitz, 1994).

In the Gallatin Valley in Montana, USA, Rees (1977, 1978) reported that after 5 years *R. conicus* had spread throughout 1280 km^2 in the valley, suggesting a rate of spread of up to 19 km $year^{-1}$. Damage to the primary, terminal flowerheads of *C. nutans* subsp. *macrocephalus* reduced their seed production, but the later secondary heads were missed (Hodgson and Rees, 1976; Rees, 1978). Interestingly, the length of the oviposition period, when mating weevils were observed, varied between years: 10 days in 1975, 39 days in 1976 (21 May–28 June) and 27 days in 1977 (Rees, 1978). Also, mortality from intraspecific larval competition increased from 23.3% to 82.5% as the

number of *R. conicus* larvae increased from 15.6 to 21.3 per head (Rees, 1977). The sunflower moth, *Homoeosoma electellum* (Hulst.), was observed to feed within the heads but, unlike the European situation, no evidence of attack on *R. conicus* was found (Rees, 1977). Thus, intraspecific competition probably limited the maximum numbers of larvae that matured per head in Montana, USA.

Feeding by *R. conicus* on North American species of *Cirsium* was first reported during this period. In Ontario, Canada, Laing and Heels (1978) reported the use of both introduced *Cirsium* species (*C. vulgare, C. arvense*) and Maw (cited in Zwölfer and Harris, 1984) reported use of the native *Cirsium flodmanii* (Rydb.) Arthur, by weevils that were originally collected from *C. nutans*. In Montana, USA, Rees (1978) reported the use of the native *Cirsium undulatum* Spreng. (wavyleaf thistle), as well as two introduced *Cirsium* spp. (*C. arvense, C. vulgare*), by *R. conicus* shipped from Mulhouse, France, and Rome, Italy, for the control of *C. nutans*. Rees (1978) found that 41% of the 517 wavyleaf (*C. undulatum*) thistles examined had *R. conicus* eggs in 1976. Although larvae occurred in the heads of only 16% of the plants, 51% of the heads on those plants had one or more larvae. Similarly, heads on 47% of 9091 Canada thistle (*C. arvense*) stems sampled had *R. conicus* eggs, and 44% of the flowers on these stems had *R. conicus* larvae (Rees, 1977). Finally, 60% of 384 bull thistle (*C. vulgare*) plants had *R. conicus* eggs, and although only 18% of the *C. vulgare* plants had live larvae in their flowerheads, 47% of the heads on those plants were infested.

Unexpectedly, egg and first instar larval mortality on *C. nutans* were high in Montana, USA, 23.3–82.5% (Rees, 1977). However, late instar larval mortality was much higher within flowerheads of the *Cirsium* species than within heads of *C. nutans* in the Gallatin Valley. For example, among the larvae that developed enough to form larval cells, subsequent mortality was 41% on the native wavyleaf thistle (*C. undulatum*), versus 31% on Canada thistle (*C. arvense*) and 62% on bull thistle (*C. vulgare*), compared with less than 3% on musk thistle (Rees, 1977). Since both Canada and wavyleaf thistles reproduce vegetatively and bull thistle was not a preferred host, Rees (1977) suggested that: 'There is no evidence to date that *R. conicus* will suppress the other thistle species.' Subsequently, Rees (1978) concluded: 'Therefore, *R. conicus* will have little effect on their [*Cirsium* spp.] populations.'

In summary, based on their interpretation of the evidence available by the early 1980s, Zwölfer and Harris (1984) argued that a combination of four factors would provide strong selection pressure against major utilization of native *Cirsium* species in North America: (i) strong preference for *C. nutans* over *Cirsium* species, especially by the biotype imported from *C. nutans*; (ii) higher larval mortality on *Cirsium* species than on *Carduus* species; (iii) smaller adult size, and so presumably lower fecundity, on *Cirsium* species than on *Carduus* species; and (iv) low population densities

of the North American *Cirsium* species would not be sufficient to support *R. conicus* population development. Thus, although the data available did not provide strong, unequivocal support for these postulated differences and feeding on native *Cirsium* species had already been reported, they concluded that despite some concern at the time (1984) it was unlikely that *R. conicus* would have an impact on North American *Cirsium* species.

Recent studies of *Rhinocyllus* (1986–1999)

Variation in phenology

In North America, recent work supports the hypothesis of latitudinal variation in activity and development of *R. conicus*. For example, in Virginia the activity of overwintered adult weevils was observed to start in mid to late April in Virginia, USA (http://www.nysaes.cornell.edu/ent/biocontrol/weedfeeders/rhinocyllus_c.html) and in Nebraska on 13 May in 1998 (S.M. Louda, unpublished results). Also, newly developed teneral adults were observed in Colorado, USA, in June and July (http://www.ag.state.co.us/DPI/publications/muskthistle.html). However, further north in south-central Alberta, Canada, overwintered adults appeared only in early June and newly emerged adults were seen in August (A.S. McClay, Alberta, 1999, personal communication). Thus, geographical differences in activity pattern can have an environmental component. Furthermore, in Europe, Aeschlimann (1999) confirmed Zwölfer's (1967) observation that the activity period of the *R. conicus* in the more southern Mediterranean climatic region was earlier than that in the more temperate climatic area of Europe. He found that the adults of *R. conicus* in the Mediterranean climate of Montpellier in southern France were active in early spring, and that their progeny started to emerge as adults in the second half of June. Alternatively, the adults of *R. conicus* in the Atlantic climate of Dordogne in south-western France were observed ovipositing later, mainly in early summer, and the new adult progeny started to emerge in mid-July. These results reinforced the suggestion of geographical intraspecific differences in *R. conicus* phenology.

Phenotypic and genetic variation in host use

In Germany, Klein (1986) studied host selection of *R. conicus*, and he concluded that the sequence in which *R. conicus* would exploit *Carduus* and *Cirsium* species within a site was predictable, using plant phenology and flowerhead availability. The earlier flowering species tended to be used first within each site. At Südpfalz, *R. conicus* used *Cirsium palustre* first, and then *C. arvense*. Near Bad Dürkheim, *R. conicus* used *Carduss nutans* first and then

C. acanthoides. In a third study site, *c.* 20 km north of Bad Dürkheim, *R. conicus* used *C. acanthoides*, *C. arvense*, *C. crispus* and then *C. vulgare* (Klein, 1986). Subsequently, Zwölfer (1988) questioned the widespread use of the biotype concept, e.g. by Zwölfer and Preiss (1983). Instead, he proposed that *R. conicus* use of *C. vulgare* in south-western France was more likely due to flowering synchrony rather than to an innate preference for *C. vulgare* over *C. nutans*.

In California, Goeden and colleagues pursued their long-term study of variation in *R. conicus* (Goeden *et al.*, 1985; Unruh and Goeden, 1987). Their studies originally suggested a mismatch between host plant and weevil biotype as an explanation for the initial failure of *R. conicus* to establish on *S. marianum* in California (Hawkes *et al.*, 1972; Goeden, 1978). Allozyme data were consistent with some degree of genetic differentiation of *R. conicus* from milk thistle (*S. marianum*) from *R. conicus* from musk (*C. nutans*) and Italian (*C. pycnocephalus*) thistles. Although only one locus (of five) showed a fixed genetic difference, allelic frequencies at the four other loci differed significantly among weevils from milk, musk and Italian thistles (Unruh and Goeden, 1987). However, Goeden *et al.* (1985) also found that *R. conicus* from *C. pycnocephalus* did oviposit on *S. marianum*, 6 years after its initial colonization of *C. pycnocephalus* when the flowerheads were nearly saturated with weevil eggs. Interestingly, the *R. conicus* from *S. marianum* began ovipositing on *C. pycnocephalus* quickly, only 1 year after its establishment, and it slowly increased its rate of oviposition on *C. pycnocephalus* over the next decade. Thus, genetic variation occurred among populations of *R. conicus*. However, the role of that variation in host use by *R. conicus* remained incompletely understood.

In Europe, Klein and colleagues performed a comprehensive allozyme and morphometric analysis of 14 widespread populations of *R. conicus*, collected from France to Israel. They showed that the populations divided into two well-differentiated, concordant groups on both sets of criteria (Klein, 1991; Klein and Seitz, 1994). The groups segregated into a north temperate group and a more southern, Mediterranean climate group, dividing at about the same latitude as the northern distribution border of the cultivated olive tree (Klein and Seitz, 1994). The *R. conicus* adults of the Mediterranean group had a narrower body, a 4 week earlier activity period, and a shorter oviposition period than did those of the temperate group. These traits – smaller size, plus earlier and shorter oviposition period – could be adaptations related to use of *Silybum* species. Klein and Seitz (1994) suggested that the two groups represented subspecies, and they proposed that the Mediterranean subspecies was equivalent to the taxon previously described as *Rhinocyllus oblongus* Cap. In summary, the evidence now suggests that differences in host use or preference between the two groups (subspecies) of weevils may have a genetic component, whereas differences in host use within each subspecies of *R. conicus* are probably related to temporal availability of flowerheads (Klein, 1986, 1991).

The temperate *R. conicus* group has been divided further by Briese (1996), into oceanic-climate and continental-climate types. He found that *R. conicus* attacked *C. pycnocephalus* in southern France mainly after *S. marianum* had finished flowering, whereas *R. conicus* from further north were associated instead with *Carduus* and *Cirsium* species. Relative use shifted east to west, from primarily *Carduus* species in the east to primarily *Cirsium* species in the west. The types also differed in pattern of activity and showed some genetic differentiation, although not as much as between the temperate and Mediterranean groups (Briese, 1996). The oceanic-climate type, which has a long pre-oviposition period after hibernation, was more closely associated with *Cirsium* species than with *Carduus* species. The long pre-oviposition feeding period would increase the coincidence of the *R. conicus* oviposition period with later flowering *Cirsium* species, like *C. vulgare*, near the Atlantic coast in France. The continental-climate type, which has a short pre-oviposition period after hibernation, was more closely associated with earlier flowering *Carduus* species than with *Cirsium* species, although some use of *Cirsium* species was observed (Zwölfer, 1967; Briese, 1996). Thus, recent research on both continents suggests that host use reflects both a hierarchy of innate host preference and the degree of synchrony between flowering and oviposition periods, with the synchrony influenced by physical conditions.

Non-target feeding on *Cirsium* species in North America

Data presented in 1985, plus work in progress at the time, raised again the issue of non-target effects in the biological control of weeds (Andres, 1985; Turner, 1985). Documented reports of feeding by *R. conicus* on native North American *Cirsium* species were published shortly after by Goeden and Ricker (1986a,b, 1987a,b) and Turner *et al.* (1987). These studies detailed the development of *R. conicus* within the flowerheads of at least 17 native *Cirsium* species in California, USA. For two of the native California species (*Cirsium californicum* Gray, *Cirsium proteanum* J.T. Howell), Unruh and Goeden (1987) used electrophoretic evidence to suggest that *R. conicus* had transferred on to them from *Carduus pycnocephalus*, rather than from *C. nutans*.

These pioneering studies of *R. conicus* on non-target native species are important, since they presage some of the recent findings in the Great Plains. For example, in samples taken in 1983–1985, Turner *et al.* (1987) found *R. conicus* in 57% of the native California *Cirsium* species sampled, representing four of the five sections of *Cirsium* native to America north of Mexico (Ownbey *et al.*, 1975). Furthermore, they were the first to record that three rare California *Cirsium* species were readily used by the weevil. In the light of these findings, they stated 'This extension of its host range is not surprising because European *Cirsium* was known to be within the host

range of *R. conicus*'. Surprisingly, they also found that the weevils from non-target *Cirsium* hosts were significantly larger than those from target *Carduus* hosts. Finally, Turner *et al.* (1987) pointed out that *R. conicus* was successful on native *Cirsium* species, and this contradicted the prevalent idea that native host-specialist insects would competitively exclude introduced biological control insects with a similar trophic niche (e.g. Peschken, 1984).

To date, *R. conicus* has been reared from flowerheads of native *Cirsium* species in every extensive survey of native *Cirsium* species in the USA: in California (Goeden and Ricker, 1986a,b, 1987a,b; Turner *et al.*, 1987; Turner and Herr, 1996; Palmisano and Fox, 1997), in Colorado (Louda *et al.*, 1997), in Montana (Rees, 1977, 1991), in Nebraska (Louda *et al.*, 1997; Louda, 1998), as well as South Dakota and Wyoming (Louda *et al.*, 1997). Because of ongoing studies of thistle–insect interactions in prairie grasslands, Louda and colleagues were the first to be able to quantify: (i) the population dynamics of host range expansion by *R. conicus* (Louda, 1998, 2000a); (ii) the consequences of feeding by native floral insect herbivores on the population dynamics of a native thistle, *Cirsium canescens* Nutt., before the host range expansion of *R. conicus* (Louda *et al.*, 1990, 1992; Louda and Potvin, 1995); (iii) the demographic effects of accelerated seed loss caused by *R. conicus* for *C. canescens* after the expansion (Louda *et al.*, 1997; Louda, 2000a; Louda and Arnett, 2000); and (iv) the indirect effects of *R. conicus* on native inflorescence insects (Louda *et al.*, 1997; Louda and Arnett, 2000; and unpublished data). The evidence from these studies on the ecological effects of *R. conicus* on native *Cirsium* species in prairies in the north-central USA is summarized below.

Thistle–insect interactions in prairies of the upper Great Plains

The ongoing studies of the floral herbivores in the population dynamics of native thistles in prairie grasslands were begun in 1976 (Lamp and McCarty, 1979, 1982a,b,c; Lamp, 1980). Four species of native *Cirsium* have been studied intensely so far: Platte thistle (*C. canescens*); its close relative, the federally listed threatened Pitcher's thistle (*Cirsium pitcheri* (Torr.) Torrey and Gray); wavyleaf thistle (*C. undulatum* (Nutt.) Spreng.); and tall thistle (*Cirsium altissimum* (L.) Spreng.). All four species are characteristic, short-lived perennial species in prairies. The local distribution of each of these native thistles is patchy (Great Plains Flora Association, 1986; Pavlovic *et al.*, 1992), and none is considered a serious weed (McCarty *et al.*, 1967).

A characteristic set of native insects feeds on or within the developing inflorescences of these thistles. On wavyleaf and Platte thistles in Sandhills prairie, the numerically most native important species damaging flowerheads are: two tephritid flies (*Paracantha culta* Wiedeman, *Orellia occidentale* [Snow]); three pyralid moths (*Homoeosoma impressale* Hulst., *Homoeosoma ardaloniphas* Goodson and Neunzig, *Pyrausta subsequalis plagialis* Haim:

G. Balogh, personal communication); and the adults of a curculionid weevil, *Baris subsimilis* Casey, whose larvae feed internally on stems and roots (Lamp, 1980; Louda and Potvin, 1995; S.M. Louda, unpublished data; C.W. O'Brien, personal communication). On Pitcher's thistle, the most common insects are the curculionid weevil (*B. subsimilis*) (C.W. O'Brien, personal communication) and two moths: the artichoke plume moth (*Platyptilia carduidactyla*; Pterophoridae) and *Homoeosoma* sp. nr. *impressale* (Pyralidae) (Louda and McEachern, 1995; and unpublished results).

In the prairie, insect herbivory on native thistles has been quantified for 25 years (Lamp and McCarty, 1979, 1981, 1982c; Louda and McEachern, 1995; Stanforth *et al.*, 1997; Jackson, 1998; Bevill *et al.*, 1999; Louda, 2000a; Louda and Arnett, 2000). These data show that feeding by native insects significantly reduces both flowerhead survival and subsequent seed reproduction by Platte, Pitcher's, tall and wavyleaf thistles. These studies have also been supplemented by experimental evaluation of the role of seed in the population dynamics of platte thistle (Louda *et al.*, 1990, 1992; Louda and Potvin, 1995), wavyleaf thistle in Nebraska sand prairie (Louda, 2000a; S.M. Louda, T. Tesar Huettner and J. Burger, unpublished results) and Pitcher's thistle in dune grasslands around Lake Michigan (Louda and McEachern, 1995; Bevill, 1998; Bevill *et al.*, 1999; and unpublished results). For Platte thistle, insect herbivores were crucial in limiting seed production, seedling establishment, local population density and lifetime fitness (Louda and Potvin, 1995). Seed availability can also limit the seedling establishment of wavyleaf and Pitcher's thistles. Thus, prior to the host range expansion by *R. conicus*, it was known that native inflorescence herbivores limited the seed production and subsequent population density of native thistles in dune grasslands (Louda *et al.*, 1990, 1992; Louda and McEachern, 1995; Louda and Potvin, 1995; Louda, 2000a; Louda and Arnett, 2000; S.M. Louda, unpublished data).

The first indication of the host range expansion by *R. conicus* on to Platte thistle and wavyleaf thistle at two long-term study sites, over 300 km apart in Nebraska sand prairie, occurred in 1993 (Louda *et al.*, 1997). Population growth of *R. conicus* since 1993 has been nearly exponential (Louda, 1998; 2000a). This host range expansion of *R. conicus* on to the two native *Cirsium* species occurred more than 20 years after the initial releases into Nebraska (1969–1974) of *R. conicus* from *C. nutans* from eastern France and north-central Italy. It is important to note that no *Carduus* species occur at the study sites in the Sandhills of Nebraska. The population growth of *R. conicus* in the Sandhills prairie nature preserves is consistent with the other evidence available on *R. conicus* use of the flowerheads of native thistles in the upper Great Plains (Louda *et al.*, 1997). Initial utilization of the native *Cirsium* species as hosts has been greatest on the early flowering species, and lowest on the high elevation (4150 m) species. Activity by *R. conicus* in Nebraska sand prairie is relatively early. Mating and oviposition by overwintered adults have been observed from mid-May to

mid-June, with the new generations emerging from mid-July to mid-August (Louda, 1998).

The initial increase of *R. conicus* in the Sandhills of Nebraska has been most significant for seed production and population demography of the earlier flowering species, Platte thistle (*C. canescens*) (Louda, 2000b). Louda (1998) hypothesized that synchrony of flowering with the period of *R. conicus* oviposition activity helped to explain this difference in initial susceptibility to *R. conicus* between the co-occurring native species, *C. canescens* and *C. undulatum*. The average number of viable seeds produced by flowerheads of Platte thistle infested with weevils in 1996 was 14.1% of that produced by similar heads with no insects or only native insects (Louda *et al.*, 1997, 1998). The weevil increased the number of seeds lost to all insects, both per head and per plant (Louda, 2000a). Since the recruitment, density and fitness of Platte thistle were previously shown to be proportional to the number of viable seeds (Louda and Potvin, 1995), the added fivefold reduction in seed imposed by *R. conicus* leads to the prediction of a severe, potentially fivefold, reduction in plant population density of this already sparse native species. Data from demography plots (1990–1999) are consistent with this prediction (Louda, 2000a; Louda and Arnett, 2000). Finally, the striking, well-documented parallels between Platte thistle and its rare congener, Pitcher's thistle (*C. pitcheri* [Torr.] Torrey and Gray) (Louda, 1994; McEachern *et al.*, 1994; Louda and McEachern, 1995; Bevill *et al.*, 1999), suggest that the same thing could happen to Pitcher's thistle if *R. conicus* were to become established in the dune ecosystem around the Great Lakes (Louda *et al.*, 1997, 1998).

Additionally, the experimental evidence now provides support for the hypothesis of indirect ecological effects of *R. conicus* on the native inflorescence insects. These insects exploit flowerheads of the same stage and size as those used by *R. conicus* (Mellini, 1951; Harris and Zwölfer, 1971; Lamp and McCarty, 1982a,c; Zwölfer and Preiss, 1983; Zwölfer and Harris, 1984). A dramatic drop in the numbers of the early tephritid, *Paracantha culta*, in Platte thistle (*C. canescens*) flowerheads was correlated with the sharp increase in the numbers of *R. conicus* from 1994 to 1996 (Louda, 1998, 2000a). In a recent experimental test, the number of *P. culta* reared per head increased dramatically when the *R. conicus* eggs were removed by hand, compared with both control flowerheads and flowerheads on which *R. conicus* eggs were experimentally augmented (Louda, 2000a; Louda and Arnett, 2000; and unpublished data).

In summary, post-release ecological studies of the use of native thistles by *R. conicus* show five main patterns: (i) occurrence is geographically widespread (Goeden and Ricker, 1986a,b; Turner *et al.*, 1987; Turner and Herr, 1996; Louda *et al.*, 1997; Palmisano and Fox, 1997); (ii) levels of use of native thistles in the central USA are high and increasing (Louda *et al.*, 1997, 1998); (iii) exponential population growth on native thistles in Nebraska showed a long (i.e. more than 20 years) lag after introduction

(Louda, 1998); (iv) both direct and indirect effects occurred; and (v) the greatest obvious impact so far has been on a species that is monocarpic, phenologically synchronized with *R. conicus*, characterized by a short flowering period, and limited in population density by seed availability. Louda and colleagues (Louda *et al.*, 1997, 1998; Louda, 2000a,b; Louda and Arnett, 2000) have argued that, although the occurrence of some feeding by *R. conicus* on North American *Cirsium* was considered likely (Zwölfer and Harris, 1984), neither the amount of that feeding nor the size of the ecological effects associated with this feeding were predictable from the data taken in pre- and early post-release studies.

Altered ecological interactions in the new environment?

One prerequisite for success in the biological control of weeds, and that may lead to unexpected pressure on non-target plant hosts in a new environment, is that the herbivore population can reach high enough densities to reduce target host plant performance and density (Gassmann, 1996). The potential for such population growth is set by a species' innate demographic characteristics. These traits, in turn, are constrained by various ecological factors, such as interactions with natural enemies and resource competitors, as well as by host plant quality, climatic variability and habitat conditions. One possible explanation for the large non-target effects of *R. conicus* in North America is that the weevil was released from ecological constraints, such as imposed by its specialized natural enemies (Zwölfer and Harris, 1984) and by its adapted, inflorescence-feeding competitors (Zwölfer, 1978, 1988). In fact, based on the oviposition patterns of the weevil in Europe, Zwölfer (1971) thought that the selection of *R. conicus* for release in North America was 'fortunate', since high egg potential and a tendency to disperse its eggs should allow *R. conicus* to exert strong pressure on its host plant, after the weevil was released from limitation by its co-evolved competitors and parasitoids. Yet, these traits also contribute to high population growth rates and high densities, and so could increase the chance of both a spillover on to nearby native *Cirsium* species and dispersal movement into areas without its targeted (*Carduus* species) hosts. Although a greater diversity of parasitoids and predators on *R. conicus* is reported in North America than in Europe, the rates of parasitism were much lower in North America than in Europe (Zwölfer and Harris, 1984). Lower parasitism rates could allow the population build-up observed for *R. conicus* in North America, on both *Carduus* species in areas of deliberate introduction (e.g. Rees, 1977, 1982) and on *Cirsium* species in areas subsequently invaded (Louda, 1998). The role of these interactions in population growth and size of *R. conicus* merit further study.

In addition, interspecific competition with other co-evolved phytophagous insects, such as *Urophora solstitialis* and *Larinus sturnus*, within

C. nutans heads in Europe is a major cause of *R. conicus* mortality, and it probably contributes to limiting population growth there (Zwölfer, 1979; Zwölfer and Harris, 1984). Although native insects utilize the inflorescences of North American *Cirsium* species, interspecific competition could be lower in North America. The Nearctic inflorescence-feeding guild is simpler (Zwölfer, 1988), and in the upper Great Plains it lacks any native cleonine weevils (O'Brien and Wibmer, 1982). A decrease in guild competitive intensity could allow high population growth rates of *R. conicus* and lead to a spillover effect on to native *Cirsium* species. However, no data are yet available to document the occurrence of such a spillover effect.

Furthermore, there is conflicting evidence on the outcome of competition of *R. conicus* with tephritid flies. On *C. nutans* in Australia, Woodburn (1996) recently found *R. conicus* is unexpectedly out-competing *U. solstitialis*, the more effective biological control agent, even though *U. solstitialis* was thought to out-compete *R. conicus* in Europe (Zwölfer, 1979). On Platte thistle in Nebraska, *R. conicus* is outcompeting the native tephritid, *P. culta* (Louda and Arnett, 2000; and unpublished results). Unfortunately, no direct tests have been done on the interaction strengths and relative effects of competitors and predators on *R. conicus* population dynamics in either Europe or North America. *R. conicus* actually has natural enemies and significant potential competitors in the native inflorescence insects in North America as well as in Europe. Thus, these interactions need more evaluation, as does the hypothesis of more rapid population growth of *R. conicus*, with potential spillover on to *Cirsium* species, in North America.

One strategy for persistence in the face of a strong competitor is to 'spread the risk' by dispersing eggs widely. In Europe, at Mulhouse, France, 98.2% of the flowerheads of *C. nutans* were attacked by *R. conicus* in 1971, and the variance-to-mean ratio of eggs per *C. nutans* head was 0.70 (Zwölfer, 1971, 1979). As a result of predation and interspecific competition, the variance-to-mean ratio of the late larval/pupal distribution was higher (2.1–3.9) than that of eggs (Zwölfer, 1979). There was a highly significant negative correlation between the developmental success of *R. conicus* and the presence of *Urophora* and *Larinus* larvae (Zwölfer, 1979). Interestingly, the variance-to-mean ratio for its competitors suggested that they were more clumped; the variance-to-mean ratios were 9.6 for *U. solstitialis* (40.5% of the heads attacked), and 1.6 for *L. sturnus* (Zwölfer, 1971, 1979). In the United States, weevil aggregation was stronger than in Europe. In Montana, following the release of 2940 adult weevils at five sites between 1969 and 1973, the 'percentage of plants with eggs on flowers' increased from 88% in 1975 to 98% and 99% in 1976 and 1977, respectively (Rees, 1978). The variance-to-mean ratio of eggs per primary (terminal) flowerhead increased from 2.4 in 1975 to 37.9 in 1976, and 61.8 in 1977 (Rees, 1978). After egg and early larval instar mortality, the variance-to-mean ratio of third instar larvae in primary heads became even greater, going from 4.5 in 1975 to 5.1–5.8 in 1976 and 1997 (Rees, 1978), perhaps as

a result of intraspecific competition. In Nebraska, Louda (1998) also reported strongly aggregated use of native thistles (*C. canescens, C. undulatum*) by adults of *R. conicus*. For example, between 1994 and 1996, the variance-to-mean ratio for adult *R. conicus* on Platte thistle (*C. canescens*) in May averaged 8.4 at Arapaho Prairie and 11.9 at the Niobrara Valley Preserve. Interestingly, the average variance-to-mean ratio for late larval/pupal number of *R. conicus* per Platte thistle plant, in the same period, increased substantially over that of the adult aggregation pattern, to 17.6 at Arapaho and 13.7 at Niobrara (S.M. Louda, unpublished data). In any case, although the data available for Europe and North America are not strictly comparable, they suggest that the distribution of the eggs and larvae of *R. conicus* on *C. nutans* tend to be more evenly dispersed in the indigenous region. Oviposition behaviour of *R. conicus*, which determines egg load distribution in Europe and North America, is also in need of further research to provide a better basis for predicting effectiveness.

Discussion

Our aim was to summarize the information available to provide a basis from which to address the general question of whether what was known, pre-release and early post-release, was sufficient to predict both the occurrence and the magnitude of impact by *R. conicus* on native thistles and their adapted floral insects. At least two main issues are confounded within the discussions over the risks associated with the deliberate introduction of exotic species for the control of exotic pest species. One issue is scientific: what evidence is required to evaluate the risks associated with various control methods, including those specific to classical biological control. The other issue is political, and can involve more rhetoric and hyperbole than fact. The evidence reviewed here can only be used to address the former issue. A review of such evidence in specific case histories is one way to learn from past mistakes in order to improve future efforts in biological control. Presumably such evidence will eventually be useful in a public context to resolve the political issue (Miller and Aplet, 1993).

Our first conclusion is that, in retrospect, the implications of the pre-release and early post-release data were that *R. conicus* would be likely to feed and develop upon some North American *Cirsium* species. The evidence suggesting the potential for problems appears to have been undervalued, reflecting both major reliance on field records to define the relative ranking among accepted hosts and the widespread acceptance of the idea of innate host preferences (biotypes) determining host-plant specificity. Our second conclusion, however, is that the studies needed to quantify the likely direct ecological consequences of that potential feeding on native species were not done, nor were studies done to examine the potential indirect effects of such feeding. Thus, in retrospect, more tests were

required to complete the assessment of the ecological implications of the documented diet breadth. It is clear, however, that economic, not environmental, risks were the main focus of the scientific assessment of *R. conicus* for the biological control of thistles. The rationale for our conclusions reflects the information presented above and the following assessment of it.

Host specificity: feeding acceptance, oviposition and larval performance

The most consistent criteria used for the evaluation of potential non-target feeding are measures of insect host specificity or diet breadth (McEvoy, 1996). Generally, these measures include: (i) feeding acceptance when starved; (ii) feeding preference when given a choice; (iii) oviposition (under choice and no-choice conditions); and (iv) subsequent larval performance on a range of related and unrelated potential host plants. Feeding tests of *R. conicus* on leaf material, both starvation (= no-choice) and preference (= choice) evaluations, were done early in the programme. In the starvation tests of *R. conicus* from *C. nutans*, the form introduced into most areas of North America including Nebraska, the intensity of feeding on most *Cirsium* species as well as weevil survival on *C. undulatum* were lower than that on *C. nutans*. However, it was clear that some *Cirsium* species were accepted, including the one North American native species that was tested, *C. undulatum* (Zwölfer, 1964, 1967; Zwölfer and Harris, 1984). In the feeding preference tests of *R. conicus* from *C. nutans* carried out by Zwölfer (1964, 1967) and summarized by Zwölfer and Harris (1984), no consistent preference was detected for *Carduus* species over *Cirsium* species (Zwölfer, 1964). Despite this, the patterns in the field, plus the conviction that *R. conicus* was divided into host-specific races, led to the interpretation that feeding on native *Cirsium* would be slight (Zwölfer and Harris, 1984).

Oviposition and subsequent larval performance were also at least partially evaluated. First, field data on host use suggested a strong association with the targeted weeds. Second, egg deposition while feeding on leaves in no-choice tests was recorded, but the meaning of such data is ambiguous. Third, the no-choice oviposition tests done in field cages with four European species (two *Carduus* spp., two *Cirsium* spp.) showed that both *Carduus* and *Cirsium* species would support complete larval development (Zwölfer, 1967; Zwölfer and Harris, 1984). The field associations received more emphasis than did the garden oviposition tests. However, although the early field data suggested that *R. conicus* generally had a strong preference for *C. nutans* over *Cirsium* species, the realized pattern of use in the field was also influenced by environmental conditions and biotic interactions as well as innate preferences. Further, the laboratory tests did not substantiate a clear preference for *Carduus* over *Cirsium per se*, but suggested a preference among species within each genus. Today, such results would be viewed as evidence that further, larger-scale tests

were warranted to quantify the factors determining the patterns and the variation in feeding impact and insect performance (relative adult survival, female oviposition, larval survival). Further choice and no-choice oviposition tests, including native North American species, to quantify relative egg loads among acceptable species, would have helped to calibrate the relative risk to *Cirsium* vs. *Carduus* species. Recently, Arnett and Louda (unpublished data) found that *R. conicus* from Nebraska still exhibited feeding and oviposition preferences for *C. nutans* over the native *C. canescens*, but also showed significant levels of acceptance of *C. canescens* even in the presence of *C. nutans*. Added no-choice oviposition and larval development tests with synchronously flowering native North American *Cirsium* species, such as *C. canescens* (Platte thistle), would also have improved quantification of the direct ecological risk to natives at low densities or in the absence of the targeted host plant. Such tests should be done as background for contemporary biological control decisions.

Given Zwölfer's (1967) early suggestion that flowering phenology probably influenced host use by *R. conicus* in the field in temperate Europe, we wonder about the real meaning of the evidence on feeding and oviposition preference. To what extent could the evidence on preference reflect environmental differences – the result of experience, physical conditions or ecological context – rather than innate, heritable differences? The data in the unpublished early reports (e.g. Zwölfer, 1964, 1967) suggested that the innate preference of *R. conicus* is likely to be only a partial predictor of host use in the field. Based on his field observations, Zwölfer (1967) suggested that a possible explanation for the variation in the use of *C. vulgare* in Italy and France 'may be found in the different phenology of the weevil populations . . . The upper Rhine Valley populations of *R. conicus* start their activity very early and are better synchronized with *C. nutans* than with *C. vulgare*, whilst the contrary may be the case with the Apennines populations.' Genetic variation exists among populations of *R. conicus* in Europe and those introduced into California (Goeden, 1978; Goeden *et al.*, 1985; Unruh and Goeden, 1987; Klein, 1991; Klein and Seitz, 1994; Briese, 1996). However, genetically determined host plant specialization is not sufficient to explain either the patterns of variation in host choice or geographical variation in that choice within the indigenous region.

Even though an ecological factor (flowering phenology) was initially suspected to be a critical parameter for predicting host use in the field, no further studies of ecological factors were performed. Instead, the reliance on patterns in the field survey and on evidence of some genetic variation, plus the inference that such variation contributed significantly to host specificity, were widely accepted (e.g. Zwölfer and Preiss, 1983; Zwölfer and Harris, 1984). In retrospect, this was unfortunate. The wide geographical range, and evidence of the associated broad ecological tolerance of *R. conicus* across Europe, as well as the feeding breadth within the Subtribe *Carduinae*, which contained native North American species, should have

stimulated further studies of the ecological parameters involved in the host choice, reproductive success and population growth of *R. conicus*.

Host specificity: larval survival and performance

The second part of most evaluations of the potential risk of non-target use involves evaluating insect host specificity by larval performance on the range of accepted potential host plants. Larval performance is generally defined by survival, development time and subsequent adult size. Lack of complete development in a well-designed test is reasonable evidence that immediate ecological effects are unlikely, although it does not preclude strong selection for adaptation under the right circumstances over the longer run (Secord and Kareiva, 1996). Slower rates of larval development have been interpreted as evidence of low impact potential (Zwölfer and Harris, 1984). However, this case history demonstrates that such evidence can underestimate the eventual use and ecological impact of the biological control agent on a less preferred non-target species (Louda *et al.*, 1997; Louda, 1998, 2000a; Louda and Arnett, 2000). With the pre-release tests in Europe and early post-release studies of *R. conicus*, for example, Zwölfer and Harris (1984) inferred that larval survival of *R. conicus* was higher, development was faster, and subsequent adults were larger on *C. nutans* than on *Cirsium* species. Thus, they concluded that 'a combination of the preference of the *C. nutans* strain of the weevil for its own host species, a high [larval] mortality and presumably low fecundity resulting from small size when reared on other thistles implies a strong selection pressure against their [*Cirsium* spp.] utilization.' They also argued that 'to overcome the negative selection pressures of adult oviposition preferences and high larval mortality, the thistle involved should be abundant. Thus it is unlikely that the normally scattered native thistles will be adopted as a prime host.'

Unfortunately, this has not turned out to be the case. Feeding and oviposition preferences were not relevant when *Cirsium* species occurred without *Carduus* species (Louda, 1998; Arnett and Louda, unpublished data). Development of larvae into adults on Flodman's thistle (*C. flodmanii*) in Canada (Maw, cited in Zwölfer and Harris, 1984), and on Platte (*C. canescens*) and wavyleaf (*C. undulatum*) thistles in Nebraska (Louda, 1998; Arnett and Louda, unpublished data) was high, though not as high as on *Carduus* species. In fact, in Nebraska, we know that larval survival and development were sufficient to lead to explosive population growth (Louda, 1998). So, the population growth and impact of *R. conicus* on Platte and wavyleaf thistles, specifically, has occurred in spite of lower larval survival and development on these species. This suggests that we should 'believe our data' (Louda, 2000a) and pursue contradictions and conflicting data if they emerge in early tests.

In summary, the preference and performance data from pre-release studies and early post-release studies suggested that some *Cirsium* species were acceptable host plants, and that development could be completed on them. Since differences in rates of acceptance and development were considered significant, and the economic imperative was primary, none of the further testing suggested by the data was undertaken. Contemporary concerns over environmental risk should make such tests standard now.

Prediction of quantitative ecological effects

Given that the preference and performance data actually did show that *R. conicus* would feed and develop on some *Cirsium* species in Europe, and so would be likely to use some *Cirsium* species in North America, were the observed population build-up and numerical impact of the weevil on the non-target North American thistles predictable? Moreover, were the indirect negative impacts on the associated native floral insects predictable? In the context of the usual contemporary testing protocols, to what extent did the standard preference and performance tests predict the ecological effects of *R. conicus* now documented? Are preference and performance tests sufficient to predict what 'intermittent feeding' under test conditions portends under new environmental conditions? The review of the data suggests that preference and performance, as evaluated in this case, were necessary but not quite sufficient to predict the numerical effects of *R. conicus* on less preferred host species under field conditions. Three types of evidence support this interpretation.

Firstly, actual testing of native North American species was clearly not a high priority of the biological control programmes before 1985, with the *Euphorbia esula* L. programme being a notable exception in North America (Pemberton, 1985a). For *R. conicus*, none of the pre-release choice tests included native North American species (Zwölfer, 1967; Zwölfer and Harris, 1984). Only two of the early post-release studies looked for development of *R. conicus* on native North American *Cirsium* species; one unpublished study in Canada on *C. flodmanii* (Maw, cited in Zwölfer and Harris, 1984) and one in Montana on *C. undulatum* (Rees, 1978). These results for native species contrast with the much more extensive evaluation of economic plant species (Zwölfer, 1964, 1967, 1969; Zwölfer and Harris, 1984).

Secondly, without evaluating the mechanisms leading to relative egg loads under field conditions in Europe, the quantitative use of various *Cirsium* species in North America could not be predicted. Observed patterns of utilization are influenced by environmental differences, and laboratory patterns of preference may or may not predict the relative amount of use among acceptable species under variable field conditions. In addition, no studies were carried out to quantify the consequences of

feeding on the less preferred populations of potential host plant species within the main regions of study, either in Europe or in North America. Such tests are required to provide some insights into the potential quantitative impact of feeding, when the preferred host is unavailable or when ecological conditions in the field shift the spectrum of host resources available. Such field data, in addition to the adult preference tests and subsequent larval performance tests, would probably have identified the potential magnitude of the non-target feeding impact of *R. conicus* on early flowering native North American *Cirsium* species that occur within the altitudinal range of the weevil.

Thirdly, comparative studies of the reproductive biology and life tables of *Rhinocyllus* 'biotypes' on non-target key species could have been used to test the hypothesis of population build-up by each 'biotype' under new environmental conditions. Comparative studies in Europe and North America of the flowerhead guild of thistle species, with and without *Rhinocyllus*, could have helped in understanding the role of horizontal effects, such as competition interference and cannibalism, on *Rhinocyllus* dynamics as well as the indirect impacts on other insects.

Thus, further studies of variable host plant use in Europe should have been used to determine the relative risk to *Cirsium* species under different environmental conditions, and to evaluate Zwölfer's (1967) early inference that ecological context could be critical. These studies could have quantified egg loads and larval success rates on less preferred plant host species, such as some *Cirsium* species, both near to and removed from the vicinity of a more preferred *Carduus* species of host plants. Similarly, these parameters could also have been tested under different physical conditions, such as those that affect phenology. Post-release comparative and experimental studies of feeding and oviposition on potentially acceptable North American *Cirsium* species were, and continue to be, merited for potentially vulnerable and rare species and for those whose flowering phenology coincides with the oviposition period of *R. conicus*. The type of studies needed could be designed on the model of the recent field assessment of the quantitative role of floral herbivores in the population density and dynamics of *C. nutans* in France (Sheppard *et al.*, 1990, 1994) or in New Zealand (Shea and Kelly, 1998), if they were extended to evaluate impacts on other acceptable species besides the one targeted for control.

Conclusions

Our review of the evidence on *R. conicus* and its relevance for resolving the controversy over the data available was required to assess the risk of deliberate introductions for the biological control of weeds, such as true thistles, and it leads to three conclusions.

First, in retrospect, the pre-release plus the early post-release data did suggest that *R. conicus* would be likely to feed, and could develop, on multiple *Cirsium* species, including important clues that North American species would be among these species. However, several factors influencing the programme at the time led the investigators to discount this evidence. These factors were: (i) a widespread acceptance of the host race paradigm; (ii) a focus on preventing damage to economic plants, which entailed selecting test plants for the screening tests which were almost exclusively cultivated plants; and (iii) a strong desire to move quickly to eliminate the weed problem. These factors contributed to a de-emphasis on the data that showed significant feeding, oviposition and development on some European and a couple of North American *Cirsium* species. A strong emphasis was placed, instead, on why the evidence was not sufficient to predict a major effect by *R. conicus* on native plant species. This latter emphasis precluded further studies, to examine conflicting data and to determine the ecological factors influencing host selection in the field.

Second, again in retrospect, the studies needed to quantify the likely magnitude of feeding and development by *R. conicus* on *Cirsium* species, and thus the ecological consequences of that feeding, were not done in this case, nor in any other up to that time as far as we are aware. Thus, a clear prediction of the intensity of direct effects, and of the type and magnitude of indirect ecological effects resulting from the feeding and potential development, was not possible. However, the early data did provide reasons to hypothesize that ecological effects might occur if *R. conicus* did include North American *Cirsium* species in its list of acceptable, phenologically exploitable host plants. For example, starvation feeding tests showed 'regular and spontaneous feeding' by *R. conicus* on at least two European *Cirsium* spp. (*C. arvense, C. vulgare*), and preference feeding tests showed higher acceptance of European *Cirsium acaule* than of *Carduus nutans*. Furthermore, larval development was also completed on European *Cirsium arvense* and *C. palustre*.

Third, the findings imply the potential for a direct, negative effect by *R. conicus* on fitness and seed production of *Cirsium* species when exploited. Interactions with other insects in the floral herbivore guild were noted, implying the potential for indirect interactions with insects in the North American inflorescence guild. However, these clues in the observations and data from pre-release and early post-release studies were not pursued. Some of the information needed could have been developed through quantitative field studies of relative egg loads on alternative hosts, under a range of environmental conditions within the geographical range of *R. conicus* in Europe. Such data would quantify the potential variation in magnitude of use of less preferred, but acceptable, host plant species. Thus, we conclude that more information could have been acquired to assess the ecological consequences and potential control effectiveness, and these data are now required under contemporary conditions.

In summary, we conclude that there were enough data suggesting that *Cirsium* species were acceptable host species to have aroused more suspicion over the potential consequences of introducing and redistributing *R. conicus* in North America without further testing. However, accurate prediction of the observed quantitative ecological effects would have required more field and laboratory experiments. Contemporary concerns now mandate such additional, pre-release testing.

Acknowledgements

We are grateful to R.W. Pemberton and U. Schaffner for their comments on an earlier draft of the manuscript. The field data collections in Great Plains prairies were assisted by many competent students and colleagues, to whom S.M. Louda is deeply grateful. C.W. O'Brien identified curculionids and G. Balogh identified the lepidopterans in the North American thistle flowerheads. Support for research on North American thistles has been provided to S.M. Louda by The National Science Foundation (DEB92-21065, DEB96-16210), the Ordway and Johnson Stewardship Fund of The Nature Conservancy and four grants (1985–1992) from the University of Nebraska Research Council.

References

Aeschlimann, J.-P. (1999) Specificity and bionomics of south-western Palaearctic biotypes of *Rhinocyllus conicus* Frölich (Col., Curculionidae), a biological control agent of Palaearctic thistles (Asteraceae) accidentally introduced to Australia. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 72, 11–22.

Andres, L.A. (1985) Interactions of *Chrysolina quadrigemina* and *Hypericum* spp. in California. In: Delfosse, E.S. (ed.) *Proceedings of the 6th International Symposium on Biological Control of Weeds.* 19–25 August 1984, Agriculture Canada, Vancouver, pp. 235–239.

Bevill, R.L. (1998) The study and management of rare plant species with special attention to the threatened Pitcher's thistle and insect herbivory. MSc. thesis, University of Nebraska, Lincoln.

Bevill, R.L., Louda, S.M. and Stanforth, L.M. (1999) Protection from natural enemies in managing rare plant species. *Conservation Biology* 13, 1323–1331.

Boldt, P.E. (1978) Foreign exploration for the biological control of *Carduus* spp. In: Frick, K.E. (ed.) *Biological Control of Thistles in the Genus Carduus in the United States.* Progress Report, USDA-SEA, Stoneville, Mississippi, pp. 11–17.

Boldt, P.E., and DeLoach, C.J. (1985) Evaluating *Rhinocyllus conicus* (Coleoptera: Curculionidae) on *Silybum marianum* (Compositae) in Texas. In: Delfosse, E.S. (ed.) *Proceedings of the 6th International Symposium on Biological Control of Weeds* 19–25 August 1984, Agriculture Canada, Vancouver, pp. 235–239.

Boldt, P.E. and Jackman, J.A. (1993) Establishment of *Rhinocyllus conicus* Frölich on *Carduus macrocephalus* in Texas. *The Southwestern Entomologist* 18, 173–181.

Briese, D.T. (1996) Phylogeny: can it help us to understand host choice by biological weed control agent? In: Moran, V.C. and Hoffmann, J.H. (eds), *Proceedings of the 9th International Symposium on Biological Control of Weeds*, 19–26 January 1996. University of Cape Town, Stellenbosch, South Africa, pp. 63–70.

Buntin, G.D., Hudson, R.D. and Murphy, T.R. (1993) Establishment of *Rhinocyllus conicus* (Coleoptera: Curculionidae) in Georgia for control of musk thistle. *Journal of Entomological Science* 28, 213–217.

Desrochers, A.M., Bain, J.J. and Warwick, S.I. (1988) A biosystematic study of the *Carduus nutans* complex in Canada. *Canadian Journal of Botany* 66, 1621–1631.

Dowd, P.F. and Kok, L.T. (1981a) Impact of larval crowding on survival of *Rhinocyllus conicus* (Coleoptera: Curculionidae). *Environmental Entomology* 10, 472–473.

Dowd, P.F. and Kok, L.T. (1981b) Predators of *Rhinocyllus conicus* (Coleoptera: Curculionidae) in Virginia. *Environmental Entomology* 10, 136–138.

Dowd, P.F. and Kok, L.T. (1982) Parasitism of *Rhinocyllus conicus* in Virginia. *Environmental Entomology* 11, 71–77.

Dowd, P.F. and Kok, L.T. (1983) Influence of soil conditions on *Carduus* thistles and development of the thistle head weevil, *Rhinocyllus conicus* (Coleoptera: Curculionidae). *Environmental Entomology* 12, 439–441.

Dunn, P.H. (1976) Distribution of *Carduus nutans*, *C. acanthoides*, *C. pycnocephalus*, and *C. crispus*, in the United States. *Weed Science* 24, 518–524.

Dunn, P.H. (1978) History of the biological control of musk thistle in North America and studies with the flea beetle *Psylloides chalcomera*. In: Frick, K.E. (ed.) *Biological Control of Thistles in the Genus Carduus in the United States*. Progress Report, USDA-SEA, Stoneville, Mississippi, pp. 1–6.

Frank, J.H. (1998) How risky is biological control? Comment. *Ecology* 79, 1829–1834.

Gassmann, A. (1996) Classical biological control of weeds with insects: a case for emphasizing agent demography. In: Moran, V.C. and Hoffmann, J.H. (eds) *Proceedings of the 9th International Symposium on Biological Control of Weeds*, 19–26 January 1996. University of Cape Town, Stellenbosch, South Africa, pp. 171–175.

Goeden, R.D. (1978) Initial analysis of *Rhinocyllus conicus* Frölich (Col.: Curculionidae) as an introduced natural enemy of milk thistle (*Silybum marianum* (L.) Gaertner) and Italian thistle (*Carduus pycnocephalus* L.) in southern California. In: Frick, K.E. (ed.) *Biological Control of Thistles in the Genus Carduus in the United States*, Progress Report, USDA-SEA, Stoneville, Mississippi, pp. 39–50.

Goeden, R.D. and Ricker, D.W. (1977) Establishment of *Rhinocyllus conicus* on milk thistle in southern California. *Weed Science* 25, 288–292.

Goeden, R.D. and Ricker, D.W. (1978) Establishment of *Rhinocyllus conicus* on Italian thistle in southern California. *Environmental Entomology* 7, 787–789.

Goeden, R.D. and Ricker, D.W. (1985) Seasonal asynchrony of Italian thistle, *Carduus pycnocephalus*, and the weevil, *Rhinocyllus conicus* (Coleoptera: Curculionidae), introduced for biological control in southern California. *Environmental Entomology* 14, 433–436.

Goeden, R.D. and Ricker, D.W. (1986a) Phytophagous insect faunas of the two most common native *Cirsium* thistles, *C. californicum* and *C. proteanum*, in southern California. *Annals of the Entomological Society of America* 79, 953–962.

Goeden, R.D. and Ricker, D.W. (1986b) Phytophagous insect faunas of two introduced *Cirsium* thistles, *C. ochrocentrum* and *C. vulgare*, in southern California. *Annals of the Entomological Society of America* 79, 945–952.

Goeden, R.D. and Ricker, D.W. (1987a) Phytophagous insect faunas of native *Cirsium* thistles, *C. mohavense*, *C. neomexicanum*, and *C. nidulum*, in the Mojave Desert of southern California. *Annals of the Entomological Society of America* 80, 161–175.

Goeden, R.D. and Ricker, D.W. (1987b) Phytophagous insect faunas of the native thistles, *Cirsium brevistylum*, *Cirsium congdonii*, *Cirsium occidentale*, and *Cirsium tioganum* in southern California. *Annals of the Entomological Society of America* 80, 152–160.

Goeden, R.D., Ricker, D.W. and Hawkins, B.A. (1985) Ethological and genetic differences among three biotypes of *Rhinocyllus conicus* (Coleoptera: Curculionidae) introduced into North America for the biological control of Asteraceous thistles. In: Delfosse, E.S. (ed.) *Proceedings of the 6th International Symposium on Biological Control of Weeds*. 19–25 August 1984, Agriculture Canada, Vancouver, pp. 181–189.

Great Plains Flora Association (1986) *Flora of the Great Plains*. University Press of Kansas, Lawrence.

Harris, P. (1984) *Carduus nutans* L., nodding thistle and *C. acanthoides* L., plumeless thistle (Compositae). In: *Biological Control against Insects and Weeds in Canada 1969–1980*. CIBC, Technical Communication No.4, pp. 115–126.

Harris, P. and Zwölfer, H. (1971) *Carduus acanthoides* L., welted thistle, and *C. nutans* L., nodding thistle (Compositae). In: *Biological Control Programmes against Insects and Weeds in Canada 1959–1968*. CIBC, Technical Communication No. 4, pp. 76–79.

Hawkes, R.B., Andres, L.A. and Dunn, P.H. (1972) Seed weevil released to control milk thistle. *California Agriculture* 26, 14.

Hodgson, J.M. and Rees, N.E. (1976) *Rhinocyllus conicus* for biocontrol of musk thistle. *Weed Science* 24, 59–62.

Hoffmann, A. (1954) *Faune de France – Coléoptères Curculionides*, Vol. 59, Editions Paul Lechevalier, pp. 521–547.

Howarth, F.G. (1983) Classical biocontrol: panacea or Pandora's box? *Proceedings of the Hawaiian Entomological Society* 24, 239–244.

Howarth, F.G. (1991) Environmental impacts of classical biological control. *Annual Review of Entomology* 36, 485–509.

Jackson, K.S. (1998) Ecological factors affecting reproductive success of tall thistle (*Cirsium altissimum*): insect herbivory, nutrient availability, and competition. MSc. thesis, University of Nebraska, Lincoln.

Jessep, C.T. (1981) Progress report on biological control of nodding thistle (*Carduus nutans*) in New Zealand. In: Delfosse, E.S (ed.) *Proceeding of the 5th International Symposium on Biological Control of Weeds*. 22–29 July 1980. CSIRO, Brisbane, pp. 635–637.

Julien, M.H. and Griffiths, M.W. (eds) (1998) *Biological Control of Weeds. A World Catalogue of Agents and their Target Weeds*. 4th edn, CAB International, Wallingford, UK.

Klein, M. (1986) Anpassung von *Rhinocyllus conicus* Fröl. (Col., Curculionidae) an allochrone Wirtspflanzensituationen. *Verhandlung der Deutschen Zoologischen Gesellschaft*. Gustav Fischer Verlag, Stuttgart, pp. 175–176.

Klein, M. (1991) Populationsbiologische Untersuchungen an *Rhinocyllus conicus* Fröl. (Col., Curculionidae). PhD thesis, University of Mainz, Wissenschafts-Verlag Maraun, Frankfurt/Main.

Klein, M. and Seitz, A. (1994) Geographic differentiation between populations of *Rhinocyllus conicus* Frölich (Coleoptera: Curculionidae): concordance of allozyme and morphometric analysis. *Zoological Journal of the Linnean Society* 110, 181–191.

Kok, L.T. (1974) Efficacy of spring releases in colonization of *Rhinocyllus conicus* for the biocontrol of thistles. *Environmental Entomology* 3, 429–430.

Kok, L.T. and Surles, W.W. (1975) Successful biocontrol of Musk thistle by an introduced weevil, *Rhinocyllus conicus*. *Environmental Entomology* 4, 1025–1027.

Laing, J.E. and Heels, P.R. (1978) Establishment of an introduced weevil *Rhinocyllus conicus* (Coleoptera: Curculionidae) for the biological control of nodding thistle (Compositae) in southern Ontario. *Proceedings of the Entomological Society of Ontario* 109, 3–8.

Lamp, W.O. (1980) Predispersal seed predation of the Platte thistle and its effect on seed production. PhD thesis, University of Nebraska, Lincoln.

Lamp, W.O. and McCarty, M.K. (1979) A preliminary study of seed predators of Platte thistle. *Transactions of the Nebraska Academy of Sciences* 7, 71–74.

Lamp, W.O. and McCarty, M.K. (1981) Biology and ecology of Platte thistle (*Cirsium canescens*). *Weed Science* 29, 686–692.

Lamp, W.O. and McCarty, M.K. (1982a) Biology of predispersal seed predators of the Platte thistle (*Cirsium canescens*). *Journal of the Kansas Entomological Society* 55, 305–316.

Lamp, W.O. and McCarty, M.K. (1982b) Observations of *Corythucha distincta* (Hemiptera: Tingidae) on Platte thistle in Nebraska. *Journal of the Kansas Entomological Society* 55, 34–36.

Lamp, W.O. and McCarty, M.K. (1982c) Predispersal seed predation of a native thistle, *Cirsium canescens*. *Environmental Entomology* 11, 847–851.

Louda, S.M. (1994) Experimental evidence for insect impact on populations of short-lived, perennial plants, and its application in restoration ecology. In: Bowles, M.L. and Whelan, C.J. (eds) *Restoration of Endangered Species*. Cambridge University Press, Cambridge, pp. 118–138.

Louda, S.M. (1998) Population growth of *Rhinocyllus conicus* (Coleoptera: Curculionidae) on two species of native thistles in prairie. *Environmental Entomology* 27, 834–841.

Louda, S.M. (2000a) Negative ecological effects of the musk thistle biological control agent, *Rhinocyllus conicus*. In: Follett, P.A. and Duan, J.J. (eds) *Nontarget Effects of Biological Control*. Kluwer Academic Publishers, Dordrecht, pp. 215–243.

Louda, S.M. (2000b) *Rhinocyllus conicus* – Insights to improve predictability and minimize risk of biological control of weeds. In: Spencer, N.R. and Nowierski, R. (eds) *Proceedings of the 10th International Symposium on Biological Control of Weeds*. 4–9 July 1999. Bozeman, Montana.

Louda, S.M. and Arnett, A.E. (2000) Predicting non-target ecological effects of biological control agents: evidence from *Rhinocyllus conicus*. In: Spencer, N.R. and Nowierski, R. (eds) *Proceedings of the 10th International Symposium on Biological Control of Weeds*. 4–9 July 1999, Bozeman, Montana.

Louda, S.M. and McEachern, A.K. (1995) Insect damage to inflorescences of the threatened dune thistle *Cirsium pitcheri*. *Bulletin of the Ecological Society of America* 76, 358.

Louda, S.M. and Potvin, M.A. (1995) Effect of inflorescence-feeding insects in the demography and lifetime fitness of a native plant. *Ecology* 76, 229–245.

Louda, S.M., Potvin, M.A. and Collinge, S.K. (1990) Predispersal seed predation, postdispersal seed predation and competition in the recruitment of seedlings of a native thistle in sandhills prairie. *American Midland Naturalist* 124, 105–113.

Louda, S.M., Potvin, M.A. and Collinge, S.K. (1992) Role of seed-feeding insect, vertebrates, and plant competition in the limitation of a native thistle population. In: Menken, S.B.J., Visser, J.H. and Harrewijn, P. (eds) *Proceedings of the 8th International Symposium on Insect–Plant Relationships*. Kluwer Academic Publishers, Dordrecht, pp. 30–32.

Louda, S.M., Kendall, D., Connor, J. and Simberloff, D. (1997) Ecological effects of an insect introduced for the biological control of weeds. *Science* 277, 1088–1090.

Louda, S.M., Simberloff, D., Boettner, G., Connor, J., Kendall, D. and Arnett, A.E. (1998) Insights from data on the nontarget effects of the flowerhead weevil. *Biocontrol News and Information* 19, 70–71.

McCarty, M.K. (1978) The genus *Carduus* in the United States. In: Frick, K.E. (ed.) *Biological Control of Thistles in the Genus Carduus in the United States*. Progress Report, USDA-SEA, Stoneville, Mississippi, pp. 7–10.

McCarty, M.K. and Lamp, W.O. (1982) Effect of a weevil, *Rhinocyllus conicus*, on Musk Thistle (*Carduus thoermeri*) seed production. *Weed Science* 30, 136–140.

McCarty, M.K., Scifres, C.J. and Robison, L.R. (1967) A descriptive guide for major Nebraska thistles. *University of Nebraska, Agricultural Experiment Station Bulletin* 493, 1–24.

McEachern, A.K., Bowles, M.L. and Pavlovic, N.B. (1994) A metapopulation approach to Pitcher's thistle (*Cirsium pitcheri*) recovery in southern Lake Michigan sand dunes. In: Bowles, M.L. and Whelan, C.J. (eds) *Restoration of Endangered Species*. Cambridge University Press, Cambridge, pp. 194–218.

McEvoy, P.B. (1996) Host specificity and biological pest control. *BioScience* 46, 401–405.

Mellini, E. (1951) Insetti del *Carduus nutans* L. II *Rhinocyllus conicus* Fröl. e *Larinus jaceae* F. (Coleoptera Curculionidae). *Bolletino Entomologica Bologna* 18, 319–349.

Miller, M. and Aplet, G. (1993) Biological control: a little knowledge is a dangerous thing. *Rutgers Law Review* 45, 285–334.

New Zealand Government (1994) *Biosecurity Act 1993*. New Zealand Government, Wellington, New Zealand.

O'Brien, C.W. and Wibmer, G.J. (1982) *Annotated checklist of the weevils (Curculionidae* sensu lato*) of North America, Central America, and the West Indies (Coleoptera: Curculionidae)*. Memoir No. 34. American Entomological Institute, Ann Arbor, Michigan.

Ownbey, G.B., Ravn, P.H. and Kyhos, D.W. (1975) Chromosome numbers of some North American species of the genus *Cirsium*. III. Western United States, Mexico, and Guatemala. *Brittonia* 27, 297–304.

Palmisano, S. and Fox, L.R. (1997) Effects of mammal and insect herbivory on population dynamics of a native Californian thistle, *Cirsium occidentale*. *Oecologia* 111, 413–421.

Pavlovic, N.B., Bowles, M., Crispin, S.R., Gibson, T.C., Herman, K.D., Kavetsky, R.T., McEachern, A.K. and Penskar, M.R. (1992) Pitcher's thistle (*Cirsium pitcheri*) recovery plan. US Fish and Wildlife Service (Region 3), Department of the Interior, Minneapolis, Minnesota.

Pemberton, R.W. (1985a) Native plant considerations in the biological control of leafy spurge. In: Delfosse, E.S (ed.) *Proceedings of the 6th International Symposium on Biological Control of Weeds.* 19–25 August 1984, Agriculture Canada, Vancouver, pp. 365–390.

Pemberton, R.W. (1985b) Native weeds as candidates for biological control research. In: Delfosse, E.S (ed.) *Proceedings of the 6th International Symposium on Biological Control of Weeds.* 19–25 August 1984, Agriculture Canada, Vancouver, pp. 869–877.

Peschken, D.P. (1984) Host range of *Lema cyanella* (Coleoptera: Chrysomelidae), a candidate for biocontrol of Canada thistle, and of four stenophagous foreign thistle insects in North America. *Canadian Entomologist* 116, 1377–1384.

Puttler, B., Long, S.H. and Peters, E.J. (1978) Establishment in Missouri of *Rhinocyllus conicus* for the biological control of musk thistle (*Carduus nutans*). *Weed Science* 26, 188–190.

Redfern, M. (1983) *Insects and Thistles.* Cambridge University Press, Cambridge.

Rees, N.E. (1977) Impact of *Rhinocyllus conicus* on thistles in southwestern Montana. *Environmental Entomology* 6, 839–842.

Rees, N.E. (1978) Interactions of *Rhinocyllus conicus* and thistles in the Gallatin Valley. In: Frick, K.E. (ed.) *Biological Control of Thistles in the Genus Carduus in the United States.* Progress Report, USDA-SEA, Stoneville, Mississippi, pp. 31–38.

Rees, N.E. (1982) Collecting, handling and releasing *Rhinocyllus conicus*, a biological control agent of musk thistle. *Agriculture Handbook* No. 579, USDA-ARS.

Rees, N.E. (1991) Biological control of thistles. In: James, L.J., Evans, J.O., Ralphs, M.H. and Child, R.D. (eds) *Noxious Range Weeds.* Westview Press, Boulder, Colorado, pp. 264–273.

Root, R.B. (1973) Organization of a plant–arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monograph* 43, 95–124.

Rowe, D.J., Kok, L.T. and Orcutt, D.M. (1985) Phytosterol requirement for propagation of *Rhinocyllus conicus* (Coleoptera: Curculionidae) on artificial diets. *Journal of Entomological Science* 20, 276–280.

Schaufuss, C. (1915) *Calwer's Käferbuch. Einführung in die Kenntnis der Käfer Europea's*, Vol. 2, pp. 1077–1079.

Secord, D. and Kareiva, P. (1996) Perils and pitfalls in the host specificity paradigm. *BioScience* 46, 448–453.

Shea, K. and Kelly, D. (1998) Estimating biocontrol agent impact with matrix models: *Carduus nutans* in New Zealand. *Ecological Applications* 8, 824–832.

Sheppard, A.W., Cullen, J.M., Aeschlimann, J.-P., Sagliocco, J.L. and Vitou, J. (1990) The importance of insect herbivores relative to other limiting factors on weed population dynamics: a case study of *Carduus nutans.* In: Delfosse, E.D. (ed.) *Proceedings of the 7th International Symposium on Biological Control of Weeds*, 6–11 March 1988, Istituto Sperimentale per la Patologia Vegetale (MAF), Rome, pp. 211–219.

Sheppard, A.W., Cullen, J.M. and Aeschlimann, J.-P. (1994) Predispersal seed predation on *Carduus nutans* (Asteraceae) in southern Europe. *Acta Oecologia* 15, 529–541.

Shorthouse, J.D. and Lalonde, R.G. (1984) Structural damage by *Rhinocyllus conicus* (Coleoptera: Curculionidae) within the flowerheads of nodding thistle. *Canadian Entomologist* 116, 1335–1343.

Simberloff, D. (1981) Community effects of introduced species. In: Nitecki, T.H. (ed.) *Biotic Crises in Ecological and Evolutionary Time.* Academic Press, New York, pp. 53–81.

Simberloff, D. (1992) Conservation of pristine habitats and unintended effects of biological control. In: Kauffman, W.C. and Nechols, J.E. (eds) *Selection Criteria and Ecological Consequences of Importing Natural Enemies.* Entomological Society of America, Lanham, Maryland, pp. 103–117.

Simberloff, D. and Stiling, P (1996) How risky is biological control? *Ecology* 77, 1965–1974.

Simberloff, D. and Stiling, P. (1998) How risky is biological control? -- reply. *Ecology* 79, 1834–1836.

Smith, L.M. and Kok, L.K. (1983) *Hyalomyodes triangulifer* (Diptera: Tachinidae) parasitizes adults of *Rhinocyllus conicus* (Coleoptera: Curculionidae). *Canadian Entomologist* 115, 1533–1534.

Smith, L.M. and Kok, L.K. (1985) Influence of temperature on the development and mortality of immature *Rhinocyllus conicus* (Coleoptera: Curculionidae). *Environmental Entomology* 14, 629–633.

Smith, L.M., Ravlin, F.W., Kok, L.K. and May, W.T. (1984) Seasonal model of the interaction between *Rhinocyllus conicus* (Coleoptera: Curculionidae) and its weed host *Carduus thoermeri* (Campanulatae: Asteraceae). *Environmental Entomology* 13, 1417–1426.

Stanforth, L.M., Louda, S.M. and Bevill, R.L. (1997) Insect herbivory on juveniles of a threatened plant, *Cirsium pitcheri,* in relation to plant size, density and distribution. *EcoScience* 4, 57–66.

Surles, W.W. (1974) Native hymenopteran parasitoids attacking an introduced weevil, *Rhinocyllus conicus* in Virginia. *Environmental Entomology* 3, 1027–1028.

Surles, W.W. and Kok, L.T. (1977) Ovipositional preference and synchronization of *Rhinocyllus conicus* with *Carduus nutans* and *C. acanthoides. Environmental Entomology* 6, 222–224.

Surles, W.W. and Kok, L.T. (1978) *Carduus* thistle seed destruction by *Rhinocyllus conicus. Journal of the Weed Science Society of America* 26, 264–269.

Surles, W.W., Kok, L.T. and Pienkowski, R.L. (1974) *Rhinocyllus conicus* establishment for biocontrol of thistles in Virginia. *Weed Science* 22, 1–3.

Surles, W.W., Pienkowski, R.L. and Kok, L.T. (1975) Mortality of the immature stages of *Rhinocyllus conicus,* a thistle head weevil, in Virginia. *Environmental Entomology* 4, 371–372.

Thomas, M.B. and Willis, A.J. (1998) Biocontrol – risky but necessary? *Trends in Ecology and Evolution* 13, 325–329.

Turner, C.E. (1985) Conflicting interests and biological control of weeds. In: Delfosse, E.S. (ed.) *Proceedings of the 6th International Symposium on Biological Control of Weeds.* 19–25 August 1984, Agriculture Canada, Vancouver, pp. 203–225.

Turner, C.E. and Herr, J.C. (1996) Impact of *Rhinocyllus conicus* on a non-target, rare, native thistle (*Cirsium fontinale*) in California. In: Moran, V.C. and

Hoffmann, J.H. (eds) *Proceedings of the 9th International Symposium on Biological Control of Weeds*, 19–26 January 1996. University of Cape Town, Stellenbosch, South Africa, p.103.

Turner, C.E., Pemberton, R.W. and Rosenthal, S.S. (1987) Host utilization of native *Cirsium* thistles (Asteraceae) by the introduced weevil *Rhinocyllus conicus* (Coleoptera: Curculionidae) in California. *Environmental Entomology* 16, 111–115.

Unruh, T.R. and Goeden, R.D. (1987) Electrophoresis helps to identify which race of the introduced weevil, *Rhinocyllus conicus* (Coleoptera: Curculionidae), has transferred to two native southern California thistles. *Environmental Entomology* 16, 979–983.

Withers, T., McFayden, R. and Marohasy, J. (2000) Importation protocols and risk assessment of weed biological control agents in Australia: the example of *Carmenta* nr. *ithacae*. In: Follett, P.A. and Duan, J.J. (eds) *Nontarget Effects of Biological Control*. Kluwer Academic Publishers, Dordrecht, pp. 195–214.

Woodburn, T.L. (1996) Interspecific competition between *Rhinocyllus conicus* and *Urophora solstitialis*, two biocontrol agents released in Australia against *Carduus nutans*. In: Moran, V.C. and Hoffmann, J.H. (eds) *Proceedings of the 9th International Symposium on Biological Control of Weeds*, 19–26 January 1996. University of Cape Town, Stellenbosch, South Africa, pp. 409–415.

Zwölfer, H. (1964) *Larinus – Rhinocyllus*. Progress Report 10, CIBC, Delémont, Switzerland.

Zwölfer, H. (1965) *A list of phytophagous insects attacking wild Cynareae species in Europe*. Progress Report 15, CIBC, Delémont, Switzerland.

Zwölfer, H. (1967) *The host range, distribution, and life-history of Rhinocyllus conicus Fröl. (Col., Curculionidae)*. Progress Report 18, CIBC, Delémont, Switzerland.

Zwölfer, H. (1969) *Additional feeding and oviposition tests with Rhinocyllus conicus Fröl.* Progress Report 24, CIBC, Delémont, Switzerland.

Zwölfer, H. (1971) Competition and coexistence in phytophagous insects attacking the heads of *Carduus nutans* L. In: Dunn, P. (ed.) *Proceedings of the 2nd International Symposium on Biological Control of Weeds*. October 1971, CAB International, Rome, pp. 74–81.

Zwölfer, H. (1978) Mechanismen und Ergebnisse der co-evolution von phytophagen und entomophagen insekten und höheren pflanzen. *Veröffentlichung naturwissenschaftlicher Verein Hamburg*, Sonderband 2, 7–50.

Zwölfer, H. (1979) Strategies and counterstrategies in insect population systems competing for space and food in flowerheads and plant galls. *Fortschitte der Zoologie* 25, 331–353.

Zwölfer, H. (1988) Evolutionary and ecological relationships of the insect fauna of thistles. *Annual Review of Entomology* 33, 103–122.

Zwölfer, H. and Harris, P. (1984) Biology and host specificity of *Rhinocyllus conicus* (Fröl.) (Col., Curculionidae), a successful agent for biocontrol of the thistle, *Carduus nutans* L. *Journal of Applied Entomology* (*Z. ang. Ent.*) 97, 36–62.

Zwölfer, H. and Preiss, M. (1983) Host selection and oviposition behaviour in west-European ecotypes of *Rhinocyllus conicus* Fröl. (Col.: Curculionidae). *Journal of Applied Entomology* 95, 113–122.